Nutrient and Carbon Dynamics in a Replacement Series of Eucalyptus and Albizia Trees

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NUTRIENT AND CARBON DYNAMICS IN A REPLACEMENT SERIES OF *EUCALYPTUS* AND *ALBIZIA* TREES

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Abstract. Tree plantations are an important component of tropical landscapes, providing wood, fuel, and perhaps carbon (C) sequestration. Primary production in wet tropical plantations is typically nutrient limited. In some Hawaiian *Eucalyptus* plantations, nitrogen (N) limitations to production are alleviated by intercropping N-fixing *Albizia* trees that may decrease available phosphorus (P). Thus, sustainable productivity and C sequestration may depend on species composition. We measured soil N and P availability and ecosystem N and C sequestration in a 17-yr-old replicated replacement series of *Eucalyptus* and *Albizia* in Hawaii. Species composition included pure plots of each species and four proportions of mixtures. Soil N availability increased with the proportion of *Albizia* in the plot, but soil P availability declined. Aboveground tree C accumulation showed a synergistic response to increasing percentage of *Albizia*, with the mixed stands having more tree C than pure stands of *Eucalyptus* or *Albizia*. In the top 50 cm of soil, total N and C increased linearly with percentage of *Albizia*. Stands with the highest percentage of *Albizia* had 230 g/m² more soil N and 2000 g/m² more soil C than stands without *Albizia*. Stable C isotope analyses showed that increased soil C resulted from differences in both tree-derived C and "old" sugarcane-derived C. Deeper soil C (50–100 cm) was a substantial fraction (0.36) of total soil C but did not vary among treatments. Our results demonstrate that tree species effects on nutrient and C dynamics are not as simple as monocultures suggest. Mixed-species afforestation increased tree and soil C accrual over 17 years, and N inputs may increase soil C storage by decreasing decomposition.

Key words: Albizia falcataria; carbon isotopes; carbon sequestration; Eucalyptus saligna; Hawaii; intercropping; nitrogen-fixing trees; sustainable forestry.

INTRODUCTION

The global coverage of tropical tree plantations increased from 21 to 43 million ha between 1980 and 1990 (Evans 1992) and estimates for 1999 exceed 60 million ha (FAO 1999). Tropical plantations are important locally for restoration of degraded and abandoned agricultural land (Parrotta 1993, Fisher 1995) and regionally as sources of wood, pulp, and fuel that relieve logging pressures on native tropical forests (Brown et al. 1997). They may be important globally as sinks for atmospheric CO_2 (Trexler et al. 1989, Lugo and Brown 1992).

Tree plantations in wet tropical climates have the potential to sequester large amounts of carbon (C) in tree biomass (Brown et al. 1986), but plantations do

not necessarily accumulate soil C (Lugo et al. 1986, Bashkin and Binkley 1998). Carbon sequestration into either soil or biomass is promoted by very high rates of net primary production (NPP); often greater than 2000 g $C \cdot m^{-2} \cdot yr^{-1}$. Such high rates of NPP typically require fertilization. On the Hamakua coast of Hawaii, the collapse of the local sugarcane industry has prompted conversion of sugarcane fields to *Eucalyptus* plantations (Davis 1994). Some experimental plantations used an intercrop of *Albizia* trees (a nitrogen-fixer), to increase nitrogen (N) supply (DeBell et al. 1989). However, recent research suggests that *Albizia* deplete the soil phosphorus (P) supply within one rotation (Binkley 1997, Binkley et al. 2000).

If N-fixing trees have large effects on N and P cycles, then species composition may greatly influence productivity and C sequestration in tropical plantations. Most studies of tree species effects on biogeochemistry use monocultures (Binkley and Giardina 1998) that do

PLATE 1. The replacement series of *Eucalyptus* and *Albizia* trees at age 17 as seen from the access road. The *Eucalyptus* stems are dark at the base and white at the top and the *Albizia* stems have white spots throughout. For scale, notice the person at the base of a Eucalyptus tree in the bottom right corner of the photo. Photograph courtesy of Dan Brinkley.

not elucidate interactions among species. Interactions in mixed-species stands could be linear, antagonistic, or synergistic relative to monocultures (deWitt 1961, Harper 1977). In the linear case, the biogeochemistry of mixed stands could be predicted from a straight line connecting values obtained in monocultures. In more complex cases, the magnitude of the biogeochemical response could be greater (synergistic) or less (antagonistic) than a linear response.

We examined interactions among N, P, and C in monocultures and mixed-species plots of *Eucalyptus saligna* (Sm.) and N-fixing *Albizia falcataria* (L.) Fosberg trees. The replacement series contained replicated plots with a constant total density and variable initial *Eucalyptus:Albizia* ratios. We addressed three questions pertinent to sustainable production and C sequestration in tropical tree plantations:

1) What is the nature of the interaction between tree species composition and biogeochemistry (linear, synergistic, or antagonistic)?

2) Do changes in soil C result from increases in plantation derived C_3-C or decreases in "old" sugarcane C_4-C?

3) How do species composition and interactions between species affect ecosystem C sequestration?

METHODS

The study area (see Plate 1) was located on the northeast coast of the island of Hawaii (19°30' N, 155°15' W) on gentle slopes (<15%) at an elevation of 480 m. Rainfall (>4 m/yr) is distributed evenly throughout the year and mean annual temperature is ~21°C. The soils are in the Kaiwiki series of thixotropic isomesic Typic Hydru-

dands. After more than 50 yr of sugarcane cultivation, the last cane crop was harvested in 1980 (for details on site history and management see Bashkin and Binkley [1998] and Binkley et al. [2000]). In 1981, the site was plowed and herbicides were used to limit regeneration. In January 1982, *Eucalyptus saligna* (Sm.) and *Albizia falcataria* (L.) Fosberg [*Albizia falcataria* is also known as *Falcataria moluccana* (Miquel) Barnaby and Grimes] seedlings were planted at a constant density (2500 trees/ha) with variable proportions of *Albizia* (0, 25, 34, 50, 66, and 100%; DeBell et al. 1989). The stands were planted in a completely randomized block design with four blocks. At 0, 4, 8, 12, 24, and 36 mo after planting, N, P, and K were applied to all plots in doses of 4, 1.8, and 3.3 g/m^2, respectively. At 55 mo, an additional 13 g/m^2 of N was applied to the pure *Eucalyptus* plots.

In January 1998, a single soil core (0.06 m diameter × 0.5 m deep) was collected from the center of every plot. In the 0, 50, and 100% *Albizia* plots, a second core was collected to a depth of 1.0 m. The soil was stored in coolers for less than five days, then weighed, homogenized by hand, and subsampled for gravimetric water content (105°C for 48 h), total N and C, and $\delta^{13}C$ analyses. Roots were removed by hand before subsampling. Bulk density was determined from the core volume, the fresh mass of the core, and the gravimetric water content of the subsample. Rock volume was negligible. Soil C and N concentrations were determined by dry combustion (LECO-1000, LECO Corporation, St. Joseph, Michigan, USA) and converted to an areal basis using the bulk density and depth of the core. The carbon isotope ratio was determined on a VG isochrom-NA stable isotope ratio mass spectrometer (VG, Middlewich, UK). There

was no evidence of inorganic C (which can confound ^{13}C:^{12}C ratios) in the samples when 0.2 mol/L HCl was applied to 10 subsamples. The soil C pools derived from sugarcane or trees (pre-sugarcane and contemporary) were calculated as in Binkley and Resh (1999). Briefly, the δ^{13}C of sugarcane ($-11.5\permil$) was determined from sugarcane tissue and the δ^{13}C of soil unaffected by sugarcane ($-25.1\permil$) was determined from soil in a nearby native forest (Bashkin and Binkley 1998). These endpoints, the δ^{13}C of the soil core, and standard mass balance equations (Vitorello et al. 1989) were used to calculate the mass of sugarcane and tree C. We call all C derived from sugarcane "old" C.

On 17 January 1998 five ion exchange resin bags were placed (0.05 m deep and 1.5 m apart) in each plot along a diagonal transect centered in the middle of the plot. The resin bags included 14 mL of anion (Sybron IONAC ASB-IPOH, Sybron International, Milwaukee, Wisconsin, USA) and 14 mL of cation (Sybron IONAC c-251 H$^+$) exchange resins in a nylon stocking. On 13 April 1998 the bags were retrieved, air dried, and extracted with 100 mL of 2 mol/L KCl. The extracts were analyzed colorimetrically for NH_4^+-N and NO_3^--N (Alpkem continuous flow autoanalyzer), and PO_4^{3-}-P (Lachat continuous flow autoanalyzer). The average total N (NH_4^+-N plus NO_3^--N) or PO_4^{3-}-P content of the five bags in each plot was used as the plot value.

We measured diameter at breast height (dbh) of each living tree in a 144 m^2 area (9 × 4 tree grid) in the center of each plot. To extend allometric equations developed for smaller trees at this site (DeBell et al. 1997), we felled six large trees (three *Eucalyptus* and three *Albizia*) and measured the length of the tree, bole diameter at 10-m intervals, the fresh mass of all branches, twigs, and leaves, and the fresh mass of bole cross sections cut at 10-m intervals. All bole cross sections and a subsample of branches, twigs and leaves, were dried (70°C) to constant mass to determine water content.

The volume of each bole segment was calculated assuming the segment was a tapered cylinder with a cross-sectional area equal to the mean of the top and bottom cross sections of that segment (Smallian's formula; Schreuder et al. 1993). Bole volume was combined with measured wood density to estimate bole biomass. Branch, twig, and foliar biomass were calculated using the fresh mass and water content. We added these six trees to data from the same site at ages 4 and 10 to develop the following equations:

Eucalyptus wood biomass = 0.0062 × dbh$^{3.3178}$

(r^2 = 0.997; n = 35)

Eucalyptus crown biomass = 0.0082 × dbh$^{2.2095}$

(r^2 = 0.952; n = 35)

Albizia wood biomass = 0.0592 × dbh$^{2.524}$

(r^2 = 0.979; n = 39)

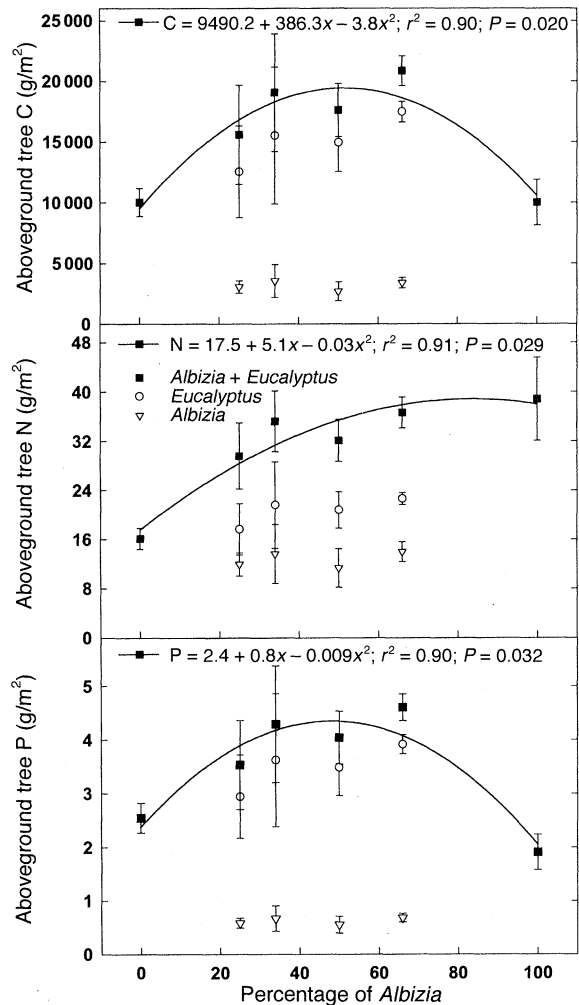*Albizia* crown biomass = 0.0381 × dbh$^{1.3701}$

(r^2 = 0.810; n = 39).

FIG. 1. Aboveground tree carbon (C), nitrogen (N), and phosphorus (P) accumulation in monocultures of *Eucalyptus* (0% *Albizia*) and *Albizia* (100% *Albizia*) and four mixed stands. Solid lines are the best-fit quadratic curve through total tree (*Albizia* + *Eucalyptus*) element accumulation. Error bars represent ±1 SE of the mean (n = 4).

The biomass of individual trees was scaled to an areal basis using the sampled area (144 m^2). Any dead or missing trees were assigned zero biomass. Tree element contents were determined by multiplying biomass by the following element concentrations: (1) wood C concentration in *Eucalyptus* from a nearby plantation (48.2%) or *Albizia* from the three trees harvested (48.0%), (2) wood N or P concentrations in *Eucalyptus* (0.04% N, 0.009% P) or *Albizia* (0.15% N, 0.007% P) determined by Binkley and Ryan (1998) using trees from these and nearby plantations, and (3) crown N and P concentrations (a biomass weighted average of leaf and twig concentrations) from the *Eucalyptus* (0.96% N, 0.097% P) and *Albizia* (2.35% N, 0.112% P) trees we harvested. Nitrogen concentrations in foliage and twigs were determined as for soils. Phos-
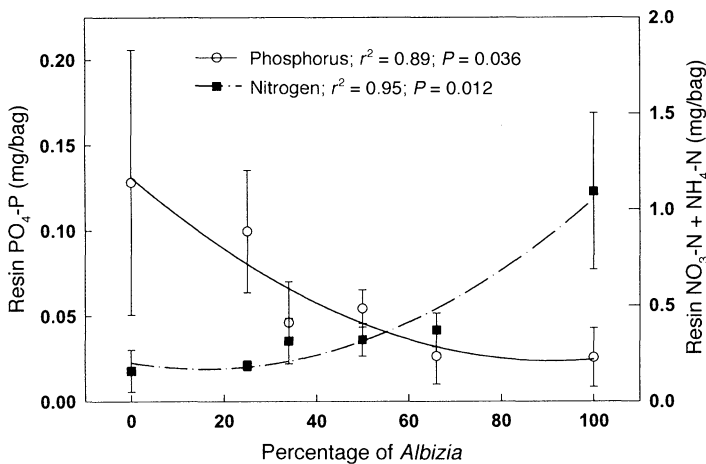
FIG. 2. Available soil phosphorus (P) and nitrogen (N), indexed by ion exchange resin bags, in monocultures of *Eucalyptus* (0% *Albizia*) and *Albizia* (100% Albizia) and four mixed stands. Lines are the best-fit quadratic curve. Error bars represent ± 1 SE of the mean ($n = 4$).

phorus concentrations were determined by block digestion (5 mL concentrated H_2SO_4 with a Na_2SO_4: $CuSO_4$ catalyst at 385°C for 4 h) followed by colorimetric analysis using the phosphomolybdate method (Murphy and Riley 1962).

All data were analyzed using linear regression with the initial planting percentage of *Albizia* as the independent variable. To determine whether a linear or quadratic model fit the data better, we decomposed the regression error into linear model error, quadratic model error, and lack-of-fit error. When the quadratic model significantly ($P < 0.10$) reduced the lack-of-fit error relative to the linear model alone, we used the quadratic model (J. ZumBrunnen, Center for Applied Statistical Expertise, Colorado State University, *personal communication*). All statistical analyses were conducted with SYSTAT 7.0 (SYSTAT 1997).

RESULTS AND DISCUSSION

Tree element accumulation and nutrient availability

The percentage of *Albizia* explained >90% of the variation in aboveground tree C, N, and P (Fig. 1). Tree

C and P were highest in the mixed-species plots and lowest in the *Eucalyptus* and *Albizia* monocultures, suggesting a synergistic relationship between species composition and tree C and P accumulation. Tree N accumulation also responded synergistically to changes in percentage of *Albizia,* but the mixed stands did not have more tree N than the pure *Albizia* stands.

The monocultures accumulated ~10 000 g/m^2 of aboveground tree C over 17 years, yielding a mean annual increment (MAI) of 588 $g \cdot m^{-2} \cdot yr^{-1}$. The MAI of the most productive mixtures (1180 $g \cdot m^{-2} \cdot yr^{-1}$) was double that of the monocultures. Working in the same stands, DeBell et al. (1997) found that tree C accretion rates reached maxima of 1100 $g \cdot m^{-2} \cdot yr^{-1}$ in pure *Eucalyptus* stands at age 4 and 1000 $g \cdot m^{-2} \cdot yr^{-1}$ in pure *Albizia* stands at age 6. The most productive mixed-species stand at age 6 (66% *Albizia*) accumulated 1200 g $C \cdot m^{-2} \cdot yr^{-1}$, similar to the MAI at age 17. Apparently, the decline in aboveground NPP with stand age was much greater for monocultures than mixed stands.

In contrast to the synergistic relationships between tree element accumulation and species composition,
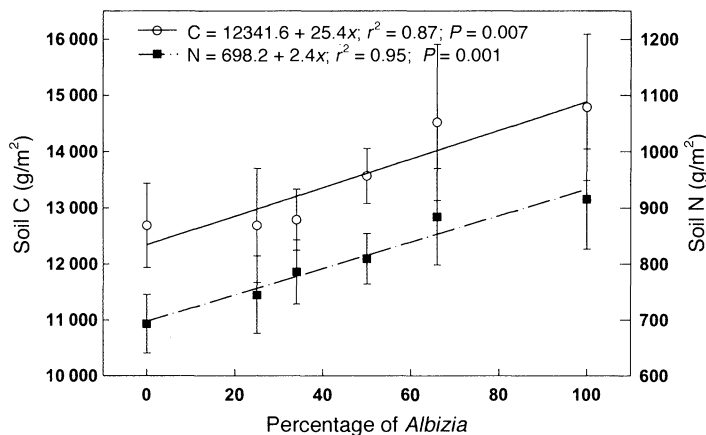

FIG. 3. Soil (0–50 cm depth) carbon (C) and nitrogen (N) in monocultures of *Eucalyptus* (0% *Albizia*) and *Albizia* (100% *Albizia*) and four mixed stands. Lines are the best-fit curve. Error bars represent ± 1 SE of the mean ($n = 4$).

FIG. 4. Soil (0–50 cm depth) organic carbon (C) in monocultures of *Eucalyptus* (0% *Albizia*) and *Albizia* (100% *Albizia*) and four mixed stands. The C_3 carbon is derived from trees, both contemporary and old, while all C_4 carbon is derived from sugarcane cultivation prior to plantation establishment. Lines are the best-fit curves. Error bars represent ± 1 SE of the mean ($n = 4$).
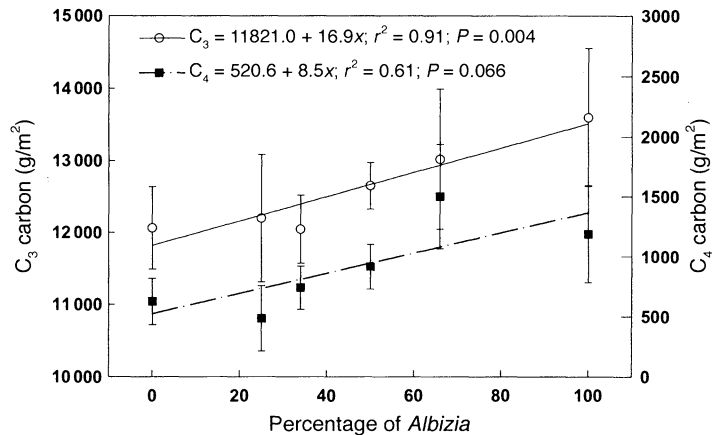
soil N and P availability had antagonistic responses to changes in percentage of *Albizia* (Fig. 2). The ion exchange resin bags showed that soil N availability increased ($r^2 = 0.95$) with increasing percentage of *Albizia* while available P decreased ($r^2 = 0.89$). The interactions between species cause nutrient availability in mixed stands to be lower than would be predicted from monoculture studies.

Soil C and N accumulation

In the top 50 cm of soil, C and N content increased linearly with increasing percentage of *Albizia* ($r^2 = 0.87$ and 0.95, respectively; Fig. 3) and the soil C:N ratio decreased from 18.3 in pure *Eucalyptus* soil to 16.2 in pure *Albizia* soil ($P = 0.06$; data not shown). *Albizia* monocultures had 230 g/m^2 (13.5 g·m^{-2}·yr^{-1}) more soil N and 2000 g/m^2 (118 g C·m^{-2}·yr^{-1}) more soil C than the *Eucalyptus* monocultures. Deeper soil (50 to 100 cm depth) contained 7984 $\pm$ 799 g C/m^2 (mean $\pm$ 1 SE) and 425 $\pm$ 42 g N/m^2; however, there were no differences among the 0, 50, and 100% *Albizia* plots at this depth ($P > 0.25$ for both C and N).

Soil C derived from sugarcane (C_4) increased linearly with increasing percentage *Albizia* (Fig. 4), indicating

either that *Albizia* trees decreased C turnover in soil or that *Eucalyptus* trees increased soil C turnover. Increasing percentage of *Albizia* also increased the amount of tree- (C_3-) derived C in the soil (Fig. 4), which could be attributed to either slower turnover of new C from trees or greater inputs of tree C. Most likely both mechanisms are important. The mechanism that inhibited decomposition of C_4-C under *Albizia* would probably operate identically on soil C_3-C.

Other research has shown that ecosystems with N-fixers accumulate soil C (Johnson 1992, Drinkwater et al. 1998; S. C. Resh, D. Binkley, and J. A. Parrotta, *unpublished manuscript*). In contrast, ecosystems without N-fixers may or may not accumulate mineral soil C during afforestation (Johnson 1992, Richter et al. 1999, Post and Kwon 2000). Bashkin and Binkley (1998) showed that planting *Eucalyptus* monocultures on abandoned sugarcane fields did not change soil C storage in Hawaii (including our site). Our results show that intercropping *Albizia* trees changes soil beneath these *Eucalyptus* plantations to a net sink for atmospheric C.

S. C. Resh, D. Binkley, and J. A. Parrotta (*unpublished manuscript*) also found that increased soil C se-

FIG. 5. The sum of aboveground tree carbon (C) or nitrogen (N) and soil (0–50 cm depth) C or N in monocultures of *Eucalyptus* (0% *Albizia*) and *Albizia* (100% *Albizia*) and four mixed stands. Lines are the best-fit quadratic or linear curves. Error bars represent ± 1 SE of the mean ($n = 4$).
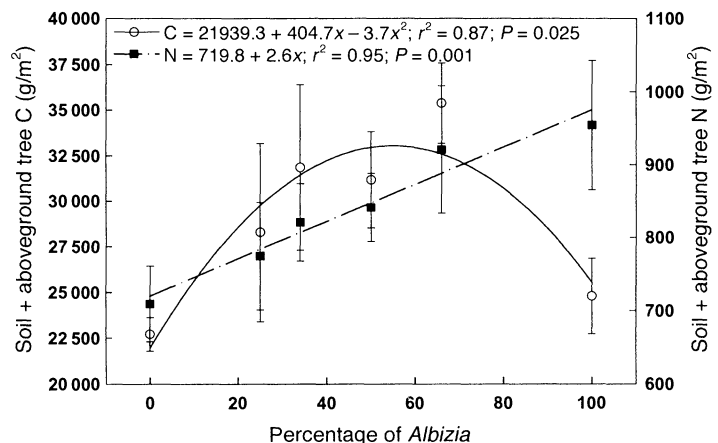
questration under N-fixers resulted, in part, from decreased turnover of old C. Their study was replicated at three additional plantations on three soil orders. It is not yet clear why N-fixer soil has more old soil C relative to *Eucalyptus.* While it is possible that *Eucalyptus* promote C turnover, we believe it is more likely that N-rich *Albizia* tissue affects humus decomposition. Many studies have shown that N additions inhibit humus decomposition (Fog 1988, Berg and Matzner 1997), and several mechanisms have been invoked to explain the result. Changes in belowground biota (Zou 1993, Garcia-Montiel and Binkley 1998) could change soil aggregation or the biomass of humus decomposers. Alternatively, N additions may stimulate humus formation simply because N is a substrate for humification (Berg and Matzner 1997).

Most research that considers N effects on C sequestration focuses on the possibility that N inputs stimulate NPP (Townsend et al. 1996, Nadelhoffer et al. 1999). Our results suggest a novel mechanism by which N additions promote C sequestration by decreasing C turnover. It is unclear whether the mechanism that promotes C sequestration in *Albizia* soil would operate similarly on large N fertilizer applications. Future research should test whether all N inputs promote soil C sequestration and the extent to which fertilizer promotes retention of old C.

Soil plus aboveground tree C and N

To gain perspective on how species interactions affect total ecosystem C (and N), we added C in the top 50 cm of soil to aboveground tree C (Fig. 5). This sum underestimates total ecosystem C because it excludes deep soil, coarse roots, and fine roots. In addition, coarse root biomass scales closely with aboveground biomass (Bernardo et al. 1998) and belowground C allocation is greater in *Albizia* monocultures than *Eucalyptus* monocultures (Binkley and Ryan 1998), so species interactions may alter belowground C and N in ways we did not measure.

Soil plus aboveground tree C was greatest in the mixed-species plots and lowest in the *Albizia* and *Eucalyptus* monocultures ($r^2 = 0.87$; Fig. 5). The mixture with the most C (32 970 g/m^2 at 55% *Albizia*) had 10 000 g/m^2 (588 g·m^{-2}·yr^{-1}) more C than the pure *Eucalyptus* plots. About 66% of sampled C was in soil in the pure *Eucalyptus* plots, 42% was in soil in the most productive mixture, and 60% was in soil in the pure *Albizia* plots. Nitrogen accumulation increased linearly with increasing percentage *Albizia* ($r^2 = 0.95$), with *Albizia* monocultures having 245 g/m^2 (14.4 g·m^{-2}·yr^{-1}) more N than *Eucalyptus* monocultures (Fig. 5). While changes in C were driven by both tree and soil C, the linear increase in N was driven by soil N, which made up >95% of the N that we sampled.

CONCLUSIONS

Most research assessing tree species effects on soils have used monocultures. Our mixed-species experi-

ments showed that species interactions can strongly influence biogeochemistry. We observed responses ranging from linear (soil N and C), to antagonistic (N and P availability), to synergistic (tree C and P). Comparisons of monocultures will not yield full insight into species effects on biogeochemistry.

Nitrogen-fixing trees appear to inhibit the decomposition of old soil carbon relative to *Eucalyptus.* If decomposition is inhibited because of greater N inputs then increased biological N-fixation, N fertilization, or N deposition may promote C sequestration by poorly understood mechanisms.

Ecosystem C sequestration was greatly affected by species composition. Changes in species composition that result from land use or climate change may have important feedbacks to terrestrial C sequestration (Pastor and Post 1988; S. R. Saleska, M. R. Shaw, M. L. Fischer, J. A. Dunne, C. J. Still, M. L. Holman, and J. Harte, *unpublished manuscript*). While we found a linear relationship between species composition and soil C storage, belowground species interactions may be more complex when coarse and fine root biomass are measured.

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